arXiv:nlin/0002033v1 [nlin.CD] 21 Feb 2000

Analysis of immune network dynamical system model with small number of degrees of freedom

SSatoko Itaya and Tatsuya Uezu

Graduate School of Human Culture,
Nara Women's University, Nara 630, Japan

Abstract

We numerically study a dynamical system model of an idiotypic immune network with a small number of degrees of freedom. The model was originally introduced by Varela et.al, and describes antibodies interacting in a body in order to prepare for the invasion of external antigens.

The main purpose of this paper is to investigate the direction of change in the network system when antigens invade it. We investigate three models, the original model, a modified model and a modified model with a threshold of concentration over which each antibody can recognize other antibodies. In all these models, both chaotic and periodic states exist. In particular, we find peculiar states organized in the network, the clustering states.

We investigate the response of the system to invasions by antigens. We find that in some cases the system changes in a positive direction when it is invaded by antigens, and the clustering state can be interpreted as memories of the invasion by antigens. Further, from the investigation of the relaxation times for invasions by antigens, it is found that in a chaotic state the average response time takes an intermediate value. This suggests a positive aspect of chaos in immune networks.

§1. **Introduction**

In this paper, we consider an immune network dynamical system model with small degrees of freedom.

First, we explain the present understanding of immune systems briefly[1, 2, 3].

The main constituents of an immune system are B-lymphocytes(B-cells) produced in the Bone marrow, T-lymphocytes(T-Cells) produced in the Thymus and free antibodies produced by B-cells. B-cells and T-cells have protein molecules called receptors on their surfaces. The receptors of B-cells are antibodies(Immunoglobulin, Ig), and antibodies recognize and connect to antigens to neutralize them. On the other hand, T-cell receptors(TcR) cannot recognize antigens, but they recognize pieces of antigens which appear on the surfaces of antigen presenting cells. When this happens, as a result, the helper T-cell expedites the immune response and the suppressor T-cell suppresses it. The killer T-cell attacks and kills a cell which is infected by viruses et.al. The receptors of B- and T-cells have proper 3-dimensional structures and these are called 'Idiotypes'. A family of B-cells which are generated from a B-cell are called 'clones'. Therefore, a clone and antibodies produced by the clone have the same idiotype.

In a human body, the total number of clones which are generated from a single B-cell are about 10 to 10^4, the total number of clones amounts to 10^8 and the number of antibodies is about 10^{20}. Thus, the repertoire of antibodies are enough to bind to any antigen. This diversity is due to the recombination and the mutation of genes.

The response to the invasion by antigens is considered as follows. When antigens enter into a body, clones which can recognize the antigen bind to it, and maturate by the help of the helper T-cells, and a part of them proliferate. Others become antibody forming cells. In the antibody forming cells, many antibodies are produced and secreted. As a result, many antibodies appear and neutralize antigens. When the neutralization completes, by the action of the suppressor T-cells, the proliferation of B-cells is suppressed and the immune response ends.

Further, in the course of the division of B-cells a part of each B-cells is preserved as a memory B-cell. When the same antigens enter into the body again, these cells rapidly differentiate into antibody forming cells and produce many antibodies in a short time. This phenomenon is called 'the secondary immune response'.

In the mechanism of the immune response explained above, a clone of the B-cells which can recognize an antigen is selected. Thus, this theory is called 'clonal selection theory' and has been confirmed experimentally.

B-cells, T-cells and antibodies die if they are not stimulated. As is mentioned

above, in a human body there are a huge number of these cells. To explain this, in 1974 N. K. Jerne proposed the so-called network view of the immune systems[1]. In his theory, these cells interact with and activate each other organizing a network. However, in 10 years after Jerne's theory appeared, the network theory was considered to fail to live up to its initial promise. This is because the theory cannot explain the correct direction of change of the system when antigens invade a body. Another reason is that since T-cells and their actions were discovered, to include these elements the original theory would lose the simplicity which attracted many researchers.

However, there are several experiments to support the network theory[4, 5]. For example, in new born mice activated lymphocytes are retained although mice are isolated from any antigen. That is, it seems that the immune system is activated by itself to prepare for the invasion of external antigens.

Thus, taking into account T-cells and their roles F. J. Varela et.al. proposed the second generation immune network model in 1991[2]. Since then, this theory has been developing [6, 7, 8].

We would like to investigate the effects of the interaction among lymphocytes and antigens, and to analyze what kind of states and structures the network can have, and to see which directions the network moves to when antigens invade the system. Also, we have interest in mathematical structures of network systems from the view point of dynamical systems.

In this paper, we study the dynamical system model of immune networks introduced by Varela et.al. In this model the essential characteristics of the real immune systems are taken into account. That is, not only antibodies, but also B-lymphocytes which produce antibodies, and the roles of T-lymphocytes, i.e., the activation and the suppression of B-lymphocytes, are included.

In reality, an immune system has a huge number of degrees of freedom. However, in this paper we focus on the Varela model with small number of degrees of freedom. Our objective is to investigate the possible states in the network and the change of these states when antigens invade the system in small systems, as a necessary step before studying the states of immune network and the immune response in large systems. Let us explain the model we treat in this paper. The constituents of the network, free antibodies and B-lymphocytes(B-cells), interact with each other through idiotypes. Let us distinguish idiotypes by index i. Between two different idiotypes i and j, there may occur an affinity, which is represented by the connectivity m_{ij}. We assume $m_{ij} = 1$ if there is an affinity between i and j and $m_{ij} = 0$ if not. m_{ij} is measurable by experiments[4, 5]. Let us denote the concen-

tration of B-lymphocytes with the i-th idiotype by b_i and that of free antibodies produced by the B-lymphocytes by f_i. These antibodies have the same idiotype as the B-lymphocytes. The sensitivity of the network for the i-th idiotype is defined as follows;

$$\sigma_i = \sum_{j=1}^{N} m_{ij} f_j, \tag{1}$$

where N is the number of idiotypes. It represents the strength of the influence by other antibodies to the i-th antibody. The number of B-lymphocytes and antibodies change in time by the following causes. Free antibodies are removed from the constituents of the network because they have a natural lifetime and also they interact with other idiotypes and are neutralized. On the other hand they are produced by B-cells as a result of the maturation of B-cells. The probability of the maturation is assumed to depend on their sensitivity σ. This effect is expressed by the function $Mat(\sigma)$. In the beginning of immune response, antibodies which interact with antigens maturate with help of T-cells. Then, it is natural to assume that the function $Mat(\sigma)$ is increasing with respect to σ when σ is small. If the number of antibodies becomes large, and the immune response comes to end, the creation of antibodies will be suppressed. Thus, for large values of σ $Mat(\sigma)$ should be decreasing with respect to σ. Thus, $Mat(\sigma)$ is assumed to have the convex profile illustrated in Fig.1.

Then, a differential equation describing the change in time of the concentration f_i of the i-th antibody can be written as

$$\frac{df_i}{dt} = -K_1 \sigma_i f_i - K_2 f_i + K_3 Mat\left(\sigma_i\right) b_i, \tag{2}$$

where K_1 is the rate of the neutralization by other antibodies, K_2 is the rate of the death of the antibody and K_3 is the rate of the creation of the antibodies by B-cells. Correspondingly B-cells carrying i-th idiotype on their surfaces decay at a given rate and proliferate when they maturate. The probability of the proliferation of B-cells is represented by the function $Prol(\sigma)$. When B-cells maturate, they begin to proliferate. Again, $Prol(\sigma)$ is assumed to be increasing with respect to σ when σ is small. When the neutralization of antigens completes, the proliferation of B-cells is suppressed by T-cells. Therefore, we assume that $Prol(\sigma)$ is decreasing with respect to σ when σ is large. Thus, $Prol(\sigma)$ also has the convex shape. Further, it seems that the proliferation of B-cells ends after their maturation ends, it is a reasonable

assumption that $Prol(\sigma)$ is shifted to right from $Mat(\sigma)$(Fig.1).
Then, the evolution equation for the concentration b_i of the B-cells with i-th idiotype can be written as

$$\frac{db_i}{dt} = -K_4 b_i + K_5 Prol\left(\sigma_i\right) b_i + K_6, \tag{3}$$

where K_4 is the death rate of the B-cells and K_5 is the rate of production of the B-cells. Further, the term K_6 is added to take into account the cells that are recruited into the active network from the bone marrow.

Here, let us see in detail how $Mat(\sigma)$ and $Prol(\sigma)$ work. First, let us consider $Mat(\sigma)$.

When the sensitivity σ is small, the B-cells are inactive. If the value of σ becomes large, they are activated to maturate by helper T-cells and begin to produce antibodies. If the value of σ increases further, the production of antibodies by B-cells is suppressed by the suppressor T-cells. As for the behavior of $Prol(\sigma)$, its behavior is similar to that of $Mat(\sigma)$. If sensitivity σ becomes large, the B-cells are proliferated by the T-cells and then they produce many antibodies. If σ increases further, this action is suppressed also by the T-cells.

Next, we describe the version of the Varela model introduced by H. Bersini and B. Calenbuhr, which we investigate and modify in this paper.

H. Bersini and V. Calenbuhr[6] have investigated a dynamical system model of immune networks in the above framework using the following functions of the maturation and the proliferation in small degrees of freedom(Fig.2).

$$Mat\left(\sigma_i\right) = \exp\left[-\left\{\frac{ln\left(\sigma_i/\mu_m\right)}{S_m}\right\}^2\right] \tag{4}$$

$$Prol\left(\sigma_i\right) = \exp\left[-\left\{\frac{ln\left(\sigma_i/\mu_p\right)}{S_p}\right\}^2\right] \tag{5}$$

In their model, B-cells and antibodies with the same idiotype are considered to form a unit. By the interaction between two units the two-unit system oscillates and the phase of one unit is opposite to that of the other.

For a three-unit network, to begin with, they considered the connection between two units in an open chain fashion(Fig.3a). Then, three units can be constrained with opposite phases each other.
Next, they considered the closed network by connecting three units as shown in Fig.3b. The connectivity matrix they used is as follows,

$$M = \begin{bmatrix} 0 & 1 & 1 \\ 1 & 0 & 1 \\ 1 & 1 & 0 \end{bmatrix} \tag{6}$$

Although each pair of units must independently comply with the imposed constraint that they oscillate in opposite phases, it isn't possible for all units to satisfy this constraint. This phenomenon has been designated by the term "frustration" and occurs in a network with a closed loop composed of an odd number of units. In general, frustration induces instability. As a result of this instability, although the time evolution of each unit resembles the motion in an open chain network, this motion does not continue more than several oscillations, and the network behaves in random way. In the following section, we investigate the characteristics of the behaviors in the original model by Bersini and Calenbuhr. In §3, we modify the original model by adopting simpler functions of $Mat(\sigma)$ and $Prol(\sigma)$ and see the effects of the choice of these functions. In the modified model, we consider a threshold over which each antibody can recognize others. This is introduced in §4. In §5, we consider the networks with more than 3 units and investigate the effect of degrees of freedom. Then the invasion of antigens is investigated in §6. Finally, §7 is devoted to summary and discussions.

§2. **The characteristics of the original model**

As is mentioned in the introduction, the system exhibits periodic oscillations for both the cases of two units and of the three-units open chain. On the other hand, for the case of the three-units closed chain, the system exhibits stable chaotic oscillations.

In this system, there always exists the following fixed point

$$(f_i, b_i) = (0, K_6/K_4), \quad (i = 1, \cdots, N), \tag{7}$$

and this point is stable. However, this solution has no meaning as a network because the interaction between units does not exist.

First, to investigate the instability of the system, we calculated Lyapunov characteristic exponents in the original model and obtained the following result for the Lyapunov spectrum,

$$(\lambda_1, \cdots, \lambda_6) = (+, +, 0, -, -, -).$$

This implies that the resultant strange attractor of this system is rather complicated in structure because there are two positive exponents.

Since this model has permutational symmetry, it should be checked whether the chaos is robust with respect to symmetry breaking perturbations. To investigate this, we gave random values around 1 to m_{ij} for $i \neq j$ with m_{ii} fixed to 0, and studied the time evolution of the system. We found that chaotic behaviors could also be obtained for asymmetric systems. Thus the chaos in this model is robust and the cause of appearance of chaos is not the symmetry of the system.

Next, to see how chaos appears in this system, we changed the strength of connectivity retaining the permutational symmetry in the system. To be specific, we set the connectivity matrix as follows,

$$M = s \times \begin{bmatrix} 0 & 1 & 1 \\ 1 & 0 & 1 \\ 1 & 1 & 0 \end{bmatrix} \tag{8}$$

and lowered s from 1 to 0. Then, we obtained the following results. See Fig.4.

Until a rather small value of $s_0 \sim 0.4$, the system exhibits chaotic motion. When s is less than s_0, a trajectory converges to the fixed point. Thus, when the connectivity is small, this model is not adequate to describe the immune network. On the other hand, when we increased s from 1, at $s \sim 1.7$ a limit cycle appears and this breaks the permutational symmetry of numbering of units.

As is shown in Fig.5(a), the phase portraits of two of the units are the same but they oscillate in opposite phases to each other. We call these units long-pulse units. One unit has smaller amplitude than those of the other two units. We call it the short-pulse unit. Let us see the characteristic feature of the oscillation of this limit cycle. Let us take notice of the time series of antibodies (Fig.5(b)). At almost all times, one of the long-pulse units has a large value of the concentration but others have small values. When the largest concentration of a long-pulse unit, say f_1, becomes small, the other two f_2 and f_3 increase taking similar values initially, then at some value of the concentrations, the concentration of the other long-pulse unit, say f_2, becomes large and the short-pulse unit f_3 becomes small. Next, when f_2 becomes small, this time f_1 and f_3 increase taking similar value and f_1 becomes

large and f_3 becomes small. Thus, it seems that the short-pulse unit plays a role of 'switching' of the activation of the long-pulse units. We call this state a clustering state.
As s is increased further, at $s \sim 4.2$. the permutational symmetry breaks completely and the medium-pulse unit appears. This state also can be called a clustering state and the role of switching is played by the short-pulse unit.
At $s \sim 4.7$, the concentrations f and b in one unit are nearly equal to 0. Since this unit merely affects other units, we do not regard this state as a clustering state.

As for the route to chaos at $s \sim 1.7$, it is considered to be Intermittency by heteroclinic intersections [1]. The sudden disappearance of chaos at $s \sim 0.4$ seems to be crisis, that is, the basin of chaos intersects with that of stable fixed point.

There are several characteristic features of this model by Bersini and Calenbuhr, those are, the topological dimension of the resultant strange attractor is three, the chaos is hyperchaos, and the switching in the clustering state. Since in this model the functions $Mat(\sigma)$ and $Prol(\sigma)$ are rather complicated, it is interesting to investigate whether these features are due to the special choice of these functions. In order to see the effect of these functions, we modify the above model by choosing simpler functions $Mat(\sigma)$ and $Prol(\sigma)$. In the next section, we go into this study.

§3. **Modified model**

We change the functions of the maturation and the proliferation as follows,

$$\begin{aligned} Mat\,(\sigma_i) &= U_1 \times [\tanh\{U_2 \times (\sigma_i - T_{lm})\} \\ &\quad - \tanh\{U_3 \times (\sigma_i - T_{um})\}], \end{aligned} \tag{9}$$

$$\begin{aligned} Prol\,(\sigma_i) &= U_4 \times [\tanh\{U_5 \times (\sigma_i - T_{lp})\} \\ &\quad - \tanh\{U_6 \times (\sigma_i - T_{up})\}], \end{aligned} \tag{10}$$

where $U_1 \sim U_6, T_{lm}, T_{um}, T_{lp}$ and T_{up} are constants. In Fig.6 we show the graphs of these functions. They look rather similar to those of the previous functions.

When the above functions are adopted as $Mat(\sigma)$ and $Prol(\sigma)$, in the case of two units, the system converges to a fixed point and in the case of the three-unit closed chain, a strange attractor appears. See Fig.7.

[1] It is reported by other authors that when some parameter is changed, this system shows Intermittency[8].

The Lyapunov spectrum for chaos becomes as follows.

$$(\lambda_1, \cdots, \lambda_6) = (+, 0, -, -, -, -).$$

Then, chaos in this system has lower dimension than that in the original system.

To investigate the onset mechanism of chaos, we drew the bifurcation diagram decreasing the magnitude of connection matrix in the same manner as in the previous section. See Fig.8.

When s is decreased from 1 or increased from 1, the transition from the strange attractor to a limit cycle takes place suddenly at $s \sim 0.94$ or $s \sim 1.5$, respectively. For the limit cycle state which appears below $s \sim 0.94$, two of three units oscillate in opposite phases, and the other unit takes negligibly small values. See Fig.9.

On the other hand, for the limit cycle state which appears above $s \sim 1.5$, two of three units oscillate in opposite phases, and the other unit oscillates with smaller values. That is, the permutational symmetry is broken in these states. The limit cycle state which appears above $s \sim 1.5$ is considered to be a clustering state as discussed in §2. See Fig.5 and Fig.10.

To see the bifurcation phenomena below $s = 1$ in detail, we calculated the first Lyapunov characteristic exponent while decreasing the strength s of the connection matrix. See Fig.11.

There exists a definite critical point. In the chaos region, time series of b_i exhibit regular oscillations interrupted by irregular motion. Thus the route to chaos from the limit cycle is Intermittency. In fact, we confirmed that in both transitions to chaos taking place at larger and smaller values of s than $s = 1$, the routes to chaos are Intermittency by heteroclinic intersections as in the original model.

As for the robustness, we checked that the system is robust with respect to permutational symmetry breaking perturbation as in the original model.

From the results in this section, we conclude that except for the topological dimensionality of the chaos, which is two in this model and three in the original one, all features are the same as those in the original model. Thus, the modified model is simpler than the original model.

§4. **The modified model with threshold**

In this section, we introduce a threshold over which antibodies can recognize antibodies and antigens. There are several reasons to take the threshold into account. One is that it seems that there exists some threshold for the concentration of

antibodies to recognize antigens. Another reason is that we would like to consider the situation in which the concentration of an antigen can become large without being recognized by antibodies for some reason. As such a situation we can consider the case that the ability of detecting antigens in the immune system becomes weak. Further, as a technical reason, introducing thresholds makes it possible to define states clearly.

When the threshold is introduced, the system exhibits various interesting behaviors.

Threshold

In the three-unit closed chain system, we introduce a threshold over which the i-th antibody can recognize other antibodies. For simplicity we take the common value f_0 of thresholds for all antibodies as follows,

$$\begin{cases} m_{ij}(t) = 1 \text{ for any } j(\neq i) & \text{when } f_j(t) \geq f_0, \\ m_{ij}(t) = 0 \text{ for any } j(\neq i) & \text{when } f_j(t) < f_0, \end{cases}$$

That is,

$$m_{ij}(t) = m_{ij}\Theta(f_j(t) - f_0), \tag{11}$$

where $\Theta(x)$ is the Heaviside function, i.e., $\Theta(x) = 1$ for $x \geq 0$ and 0 for $x < 0$. Hereafter, m_{ij} in the right hand side of the above equation is fixed to the value in eq.(6). We scanned the value of the threshold f_0 every 5 values and obtained the following behaviors of the system.

$f_0 = 5 \sim 15$	Limit cycles. The concentrations of B-cells of two units are always greater than the threshold and the other is always less than it.(Fig.12)
$f_0 \sim 20$	Limit cycle with period two.
$f_0 = 25 \sim 40$	Chaos. Fig.13
$f_0 = 45 \sim 50$	Limit cycles. Clustering state.(Fig.14).
$f_0 \geq 55$	Fixed point.

For $f_0 = 5 \sim 50$, the system is in the clustering state which is defined in §2. In this state, each of three units oscillates taking values below and over the threshold. Two long-pulse units have longer duration over the threshold and the short-pulse unit has shorter duration.

For the time series analysis, we define the on-off time series as follows. Let us associate 0 or 1 with each unit according to the value of f_i, that is, 0 for $f_i < f_0$ and

1 for $f_i \geq f_0$. We call the former the off-state and the latter the on-state, and the sequence of 0 and 1 as a function of time the on-off time series. As shown in Fig.15, at almost all times, there exists only one on-state, and whenever the long-pulse unit changes from the on-state to the off-state, the short-pulse unit becomes the on-state. That is, the short-pulse unit plays a role of switching. This is the same phenomenon as observed in §2 and §3.

Thus, this phenomenon takes place in all models we studied. The cause of this phenomenon is ascribed to the nature of the interaction. We discuss this in the final section.

If we take an initial state such that all units are less than the threshold, the system converges to the fixed point. On the other hand, if at least one unit exceeds the threshold initially, then the system goes to the clustering state.

We investigated the bifurcation structure when the system is in the clustering state for $f_0 = 50$. To see the bifurcation structure clearly, we introduce the strength of effective interaction $< I_{ij} >$. $< I_{ij} >$ is defined by the following relation,

$$< I_{ij} > \;=\; \lim_{T\to\infty} \frac{1}{T} \int_0^\infty dt I_{ij}(t). \tag{12}$$

$$I_{ij}(t) = m_{ij}(t) + m_{ji}(t). \tag{13}$$

For example, if $f_1(t) \geq f_0, f_2(t) \geq f_0$ and $f_3(t) < f_0$, then $m_{21}(t) = m_{31}(t) = 1, m_{12}(t) = m_{32}(t) = 1$ and $m_{13}(t) = m_{23}(t) = 0$. Thus, $I_{12}(t) = I_{21}(t) = 2, I_{13}(t) = I_{31}(t) = 1$ and $I_{23}(t) = I_{32}(t) = 1$. See Fig.16.

As s is lowered, the initial periodic state for $s = 1$ becomes chaos at $s \sim 0.93$, and the permutational symmetry is recovered. See Fig.17. When s is lowered further, the periodic state appears again at $s \sim 0.52$(Fig.18).

We show the bifurcation diagram (Fig.19) and the s dependence of $< I_{ij} >$ (Fig.20).

Here, we summarize the result.

1. $s_1(\sim 0.93) \leq s \leq 1$. Limit cycle. (Clustering state.) Fig.14.
   There occurs clustering and there are two groups of $< I_{ij} >$. That is, the interaction between two long-pulse units, say I_{LL}, and the interaction between the long-pulse unit and the short-pulse unit , say I_{LS}. Typical values are

$$I_{LL} \sim 0.83,\ I_{LS} \sim 0.8.$$

2. $s_2(\sim 0.52) \leq s \leq s_1$. Chaos. Fig.17.
   All $< I_{ij} >$ take almost the same values. The typical value is

$$I_{LL} \sim I_{LS} \sim 0.85.$$

3. $s_3(\simeq 0.4) \leq s \leq s_2$. Limit cycle. Fig.18.
   As for the usual time series, one unit takes negligibly small values and the other two units oscillate in opposite phases. Then, the symmetry of this state is broken and two units always exceed the threshold and the other never exceeds the threshold. Reflecting these behaviors, the values of $< I_{ij} >$ are divided into two groups, - in one group $< I_{ij} >$ tends to 2 and in the other it tends to 1 as $s \to s_3$. Since one unit does not affect other units, it is not appropriate to call this a clustering state.

4. $0 < s \leq s_3$. Fixed point.
   There is no meaning of a network.

From these observations, we note that $< I_{ij} >$ can be used to distinguish the clustering state from other behaviors. In particular, in the state of chaos, all the $< I_{ij} >$ take almost the same value.

The Lyapunov spectrum for chaos is

$$(\lambda_1, \cdots, \lambda_6) = (+, 0, -, -, -, -),$$

and is the same as in the modified model.

The routes to chaos at $s \sim 0.93$ and $s \sim 0.52$ are also Intermittency by the heteroclinic intersections.

§5. **The effect of the degree of freedom**

Here we investigate the behaviors of the network when the number of units is increased for the modified model with threshold. We assume that there exists interactions between any two units and the connectivity matrix is symmetric, i.e., $m_{ij} = m_{ji} = 1$ for any i and j $(i \neq j)$.

We investigated the cases of $N = 3, 4, \cdots, 10$. In Fig.21 and 22, we show phase portraits for several cases.

The clustering state occurs in all cases. However, it seems that it takes place more frequently in the case of the odd number of units in the parameter ranges which we investigated. (Fig.21, 22)

Indeed, for $N = 3, 5, 7$ and 9 and when the threshold is the same for all units, clustering takes place and for $N = 4, 6, 8$ and 10, it does not. In the figures 21(b) and 22(b), we show the effective interactions schematically. In these figures thick lines denote large strength, thin lines represent medium strength and dotted lines represent small strength. When the clustering occurs, the system is in a limit cycle state, and the number of the long-pulse units is larger by one than that of the short-pulse units. There are three values of the strength of the effective interaction in the system. See Fig.22(b). The strength of the effective interaction takes the largest value I_{LL} between two long-pulse units, the smallest I_{SS} between two short-pulse units and intermediate value between the long-pulse unit and the short-pulse unit. When the clustering does not occur in the system, the strengths of the effective interactions are almost the same. See Fig.21(b).
We show the on-off time series for $N = 3$(Fig.15), $N = 5$(Fig.23), $N = 4$(Fig.24(a)) and $N = 6$(Fig.24(b)).

From these figures we note that for $N = 3$ and 5, there are only two types of units, i.e., long-pulse units and short-pulse units. On the other hand, for $N = 4$ and 6, in any unit, the duration time of the on-state varies in time. To clarify this we calculate the histogram of the duration time. See Fig.25, 26, 27, 28. In the case of odd number of units, we notice that the duration time T_L for the long pulse unit is nearly twice as the duration time T_S for the short-pulse unit. On the other hand, in the case of even member of units, although there are various duration times, we can find two peaks of the long duration time and the short one. That is, in the chaotic state, the role of each unit changes dynamically.

§6. **The invasion of antigen**

Hereafter, we consider the response of the system to the invasion of antigens in the modified model with threshold.

Case 1

We consider the clustering state in the 3-units closed network. Suppose that external antigens similar to antibodies f_1 invade the system. Let us denote the concentration of the antigen by a_1 and that of the corresponding antibodies by f_1. Then, antibodies f_2 and f_3 recognize the antigens, because a_1 resemble f_1. However, in general the antibodies f_1 cannot recognize the antigens. See Fig.29.

Further, we assume that the antigen does not proliferate by itself [2]. Thus, the

[2]This restricts the type of antigens. For example, pollen are one candidate.

differential equation for the antigen is given by

$$\frac{da_1}{dt} = -K_1\sigma_a(t)a_1 + K_7, \tag{14}$$

where $\sigma_a(t) = m_{12}(t)f_2(t) + m_{13}(t)f_3(t)$. Here, we assume that the antigens enter into the system at a rate K_7 per unit time. On the other hand, since antibodies f_2 and f_3 interact with the antigens, σ_2 and σ_3 become $\sigma_2 = m_{21}(f_1 + a_1)\Theta(f_1 + a_1 - f_0) + m_{23}(t)f_3$ and $\sigma_3 = m_{31}(f_1 + a_1)\Theta(f_1 + a_1 - f_0) + m_{32}(t)f_2$, respectively. Then using these σs the equations for antibodies and B-cells are the same as the previous ones.

Now, let us see what happens in this system. The behavior of the system depends on the increase rate of the antigen K_7. If K_7 is large enough, say $K_7 > K_7^u(\sim 1.2)$, the concentration of the antigen a_1 increases infinitely and the system is completely invaded and destroyed by the antigen[3]. If K_7 is less than some value, say $K_7 < K_7^l(\sim 0.7)$, the system copes with the antigens completely. The number of antigens finally become small and the system settles near to a clustering state depending on the initial condition. Thus, in this case there is no memory of the invasion by antigens.

If we set K_7 between K_7^l and K_7^u, e.g., $K_7 = 0.7$, a_1 does not increase infinitely but oscillates in some range of concentration. The time series of a_1 and the phase portrait of the system are drawn in Fig.30 and 31, respectively.
Although the system is modified because of the invasion by the antigen, for $K_7^l < K_7 < K_7^u$, it still keeps the nature of the network as a whole. In the resultant state, the duration time of the on-state for f_2 and f_3 are longer, i.e., the units 2 and 3 are long-pulse units.

Now, let us study the response time of the system when $K_7 = 0$. To do this, starting from $a_1 = 50$ we calculated the relaxation time in which the concentration of the antigen becomes negligibly small. See Figure 32.

From this figure, we note that the response time is shorter in the state in which the units 2 and 3 are in the long-pulse units. In the resultant attractor the units 2 and 3 are the long-pulse units. This result implies that the system modifies itself so as to neutralize the antigen as effectively as possible. Thus, it seems that the resultant state can respond much better than other states.
Therefore, we can state that the resultant attractor is viewed as a kind of memory

[3] The system tends to the fixed point

of the invasion by the antigen.[4]

Further, we scanned the initial value of A_7 with K_7 fixed to 0.7. For $A_1 < 288$, the system settles to a clustering state. On the other hand, for $A_1 > 288$ the system tends to a fixed point and the network collapses.

Case 2

Next, we consider the case that an antigen A_1 interacts only with the antibody f_1 in the 3-unit closed network. (Fig.33).

In this case, we set the thresholds depending on units in order to obtain clustering states. Here, we introduce new notations of thresholds, $f_{i,0}(i = 1 \sim 3)$, $g_{1,0}$ and $g_{A,0}$ as follows. $f_{i,0}$ is the threshold over which the i-th antibody recognizes other antibodies. $g_{1,0}$ is the threshold over which the antibody f_1 recognizes the antigen and $g_{A,0}$ is the threshold over which the antigen A_1 recognizes the antibody f_1. Then the equation for the antigen A_1 is

$$\begin{aligned} \frac{dA_1}{dt} &= -K_1\sigma_A(t)A_1 + K_7, \\ & \sigma_A(t) = \Theta(f_1 - g_{1,0})f_1. \end{aligned} \tag{15}$$

The first term expresses the decrease of the antigen by neutralization by the antibody 1 and the second term represents the continuous invasion of the antigen. The sensitivity σ_i of the i-th unit is modified to

$$\sigma_i = \sum_{j=1}^{n} m_{ij}\Theta(f_j - f_{j,0})f_j + l_i A_1 \Theta(A_1 - g_{A,0}), \tag{16}$$

where l_i is the strength of the interaction between f_i and A_1. We put $l_i = s_A\delta_{i,1}$, where $\delta_{i,1}$ is the Kronecker's delta. The behavior of this network strongly depends on the thresholds, the value of connectivity s_A, the initial value of the antigen A_1 and the rate of invasion of the antigen K_7. If these values are taken appropriately, the concentration of the antigen oscillates in some range. See Fig.34.

As in the case 1, the unit 1 which can interact with the antigen is activated and finally settles near to the long-pulse state. See Fig.35.

It turns out that the relaxation time of the concentration of the antigen is comparable in this state with in the state where the unit 1 is in the short-pulse state.

[4] We use the term 'memory' to express the change to the positive direction of the system under the invasion by the antigens. It should not be confused with creation of memory B-cells.

See Fig.36.

When we compare this result with the result in the case 1, it is considered that the number of units which can interact with antigens is important for the relaxation time.

Case 3

Now, let us consider the network with 4-units. We assume that the antigen (a_1) has a similar three-dimensional structure to the antibody 1 and then can interact with the unit 2, 3 and 4, but cannot interact with the unit 1. See Fig.37.

The differential equation for the antigen is

$$\frac{da_1}{dt} = -K_1\sigma_a(t)a_1 + K_7, \tag{17}$$

$$\sigma_a(t) = (m_{12}(t)f_2 + m_{13}(t)f_3 + m_{14}(t)f_4). \tag{18}$$

For the unit i, the differential equations are

$$\frac{df_i}{dt} = -K_1\sigma_i(t)f_i - K_2f_i + K_3Mat(\sigma_i(t))b_i, \tag{19}$$

$$\frac{db_i}{dt} = -K_4b_i + K_5Prol(\sigma_i(t))b_i + K_6, \tag{20}$$

$$\sigma_1(t) = \sum_{j\neq 1} m_{1j}(t)f_j, \tag{21}$$

$$\sigma_i(t) = m_{i1}(f_1 + a_1)\Theta(f_1 + a_1 - f_0) + \sum_{j\neq 1} m_{1j}(t)f_j, \quad i \neq 1. \tag{22}$$

If we break the symmetry of the connectivity matrix by lowering the threshold of one of the four units, for some initial condition this unit stays in the short-pulse state and other units stay in the long-pulse states, and so the clustering takes place(Fig.38). For some other initial conditions, chaotic states appear. That is, in this case chaos and the clustering states coexist.

From the result of the case 1, it is expected that the relaxation time of the system is short when the unit which resembles the antigen is in the short-pulse state. Further, from the result of the case 2, it is expected that the more is the number of units which interact with the antigens, the shorter is the relaxation time. Thus, here we investigate the relaxation time for the following three cases.

Case a. The unit 1 is in the short-pulse state.

Case b. The unit 1 is in the long-pulse state.

Case c. The system is chaos.

We show the result in Fig.39.

The relaxation time τ_a for the case a is shortest and τ_b for the case b is longest. τ_c for the case c is in between τ_a and τ_b. From this result, it is considered that chaos is more effective than the clustering states to prepare for various types of antigens.

§7. **Summary and discussions**

In this paper, we studied the three models of the immune network for small number of degrees of freedom $N \sim 10$, the original model introduced by Bersini et.al., the modified model with different functions of the maturation and the proliferation of B-cells from those of the original model, and the modified model with a threshold over which antibodies can recognize other antibodies and antigens. First, we summarize common characteristics of these models.

In these models there exist limit cycle states and chaotic states. We investigated bifurcation structures obtained by changing several parameters and found that the transitions to chaos are Intermittency by heteroclinic intersections.

There is a peculiar type of limit cycle. In this limit cycle, the permutational symmetry of the system is broken and concentrations of antibodies and B-cells oscillate in a characteristic manner. We call this the clustering state.
In the clustering state, for example in the three-unit system, there are two long-pulse units in which the concentrations of antibodies are large and one short-pulse unit in which the concentration of the antibody is small. Two long-pulse units oscillate in anti-phase to each other. At almost all times, only one unit has a large concentration of the antibody. The short-pulse unit plays a role of "switching" the long-pulse units which take the large concentrations.

On the other hand, in the state of chaos, no such explicit division of roles exist, but each unit changes its role dynamically. That is, in chaos, a dynamical change of roles takes place.

We investigated the invasion by antigens when the clustering takes place. We found that when the number of antigens is not too many and interaction between antigens and antibodies continues for an appropriate period, the unit which can interact with antigens settles near to the long-pulse unit after the concentration of antigens is reduced to small values in some range of a parameter.

By investigating the relaxation time, we found that in the clustering state the relaxation time depends on what state the system stays in. In the case 1 that the two

units interact with antigens the relaxation time is short or long when the unit which interacts with antigens is in the long-pulse unit or short-pulse unit, respectively. On the other hand, in the case 2 that only one unit interacts with antigens the relaxation time takes similar value both in the long-pulse unit and in the short-pulse unit. Thus, if many units can interact with antigens by the invasion of the antigens the system moves to the state in which the response to antigens is most efficient. Thus, the clustering state is considered to be a memory of the invasion by antigens.

Further, we checked that the system is robust against the symmetry breaking perturbations. Chaotic and periodic states change only a little by these perturbations.

As for the modified model with thresholds, we observed a interesting feature. The feature is the positive aspect of chaos in response to the invasion by antigens. In this model there is the coexistence of chaos and clustering states when the thresholds are chosen appropriately depending on units. In the response to the antigen invasion, we found that the relaxation time in chaotic state takes an intermediate value between the large and the small response times in the two types of clustering states. This suggests a positive aspect of chaos in immune networks, that is, the possibility that chaos may cope with the invasion by any kinds of antigens equally well.

Now, let us discuss the cause of the appearance of clustering state. This is related to the mechanism of the switching of long-pulse units or the dynamical role change. Let us consider the 3-unit closed chain. See Fig.5(b), 10(b) and 40. In the present interaction, any two units tend to oscillate in opposite phases. If the concentration of the antibody in one unit, say f_1, increases, then the sensitivities of other two units become large. By this, the second terms of the differential equations for f_2 and f_3 become large and f_2 and f_3 decrease. This is a kind of 'winner takes all' mechanism. Then, the sensitivity σ_1 becomes small. Thus, when f_1 becomes large, the third term of the differential equation for f_1 becomes small compared to the other two terms. Thus, next f_1 begins decreasing. This causes the decrease of σ_2 and σ_3 and the increase of f_2 and f_3. Since f_2 and f_3 begin to increase from small values, these take similar values. However, when these become rather large, two units are forced to stay in states with opposite phases each other. Thus, one increases further and the other decreases. At this stage, for the clustering state, the increasing unit is fixed to the long-pulse unit, but for chaos, it is not fixed and the dynamical change of the switching role takes place. Therefore, the behavior of the switching is due to the 'winner takes all' mechanism and the 'anti-ferro' type interaction between any

two units.

Next, let us discuss the causes of different behaviors between the original model and the modified model without threshold.
We studied influences of each of the terms in the 3-unit closed chain system. We pay attention to the unit 1 only, (f_1,b_1), because we consider the case that the system has the permutational symmetry. The differential equations of f_1 and b_1 are

$$\frac{df_1}{dt} = -K_1\sigma_1 f_1 - K_2 f_1 + K_3 Mat\left(\sigma_1\right) b_1 \tag{23}$$

$$\frac{db_1}{dt} = -K_4 b_1 + K_5 Prol\left(\sigma_1\right) b_1 + K_6 \tag{24}$$

Here, we denote each term in the above equations as follows.

$$\begin{aligned} F_1 &= -K_1\sigma_1 f_1, \\ F_2 &= -K_2 f_1, \\ F_3 &= K_3 Mat\left(\sigma_1\right) b_1, \\ B_1 &= -K_4 b_1, \\ B_2 &= K_5 Prol\left(\sigma_1\right) b_1, \\ B_3 &= K_6. \end{aligned} \tag{25}$$

We compare the time sequence in the original model with that in the modified model. See Fig.41,42.

In these figures, solid lines denote F_1 and B_1, large dotted lines represent F_2 and B_2, small dotted lines represent F_3 and B_3, respectively. We note that the terms concerning the maturation and the proliferation give the biggest influence on the behaviors of the system in both the models. In the original model these terms increase and decrease more rapidly than in the modified model.
The chaos in the original model is hyperchaos but that in the modified model is not hyperchaos. The complexity and the large topological dimensionality for chaos in the original model seem to be due to sharp behaviors of these functions. However, to clarify the influence of the choice of these functions, it is necessary to perform further investigation. This is left to a future study.

We considered the threshold over which the antibodies can recognize other antibodies. We can also consider a threshold over which the antigen can be recognized by other antibodies. This is another situation to be investigated.

In this study, we investigated three cases of invasions by antigens. In these cases, we have interest in the generic behaviors of the system when the several parameters are changed, e.g., the initial values of antigens or the input rate of the antigen K_7, etc. We found that in some cases the system changes in a positive way, that is, in the resultant state the relaxation time becomes shorter if there are plural units which interact with antibodies. There exists a kind of memory in the system. From the perspective of the real immune network, the existence of memory states and the response to the invasion by antigens in a system with large number of degrees of freedom are very interesting problems. These will be studied in the future.

Acknowledgements

The authors are grateful to S. Tasaki, S. Kitsunezaki and P. Davis for valuable discussions. One of the authors(S. I.) would like to thank Professor Y. Kuramoto and the members of his research group in Kyoto University for valuable discussions.

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Figure captions

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